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THE STATUS OF BOTHRIOCIDARIS

BY ROBERT TRACY JACKSON

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No. 13.— *The Status of Bothriocidaris*

BY ROBERT TRACY JACKSON

My friend Dr. Th. Mortensen, in a recent paper, has taken the position that the ancient Ordovician genus *Bothriocidaris* is not an echinoid but a cystoid. The student of fossil invertebrates rarely has students of recent forms enter his field, and it is gratifying that a leading authority on recent Echini should undertake the study of fossil forms. That fossil and recent should be studied together for their mutual elucidation is, I believe, of fundamental importance. The student of recent Echini, in undertaking the study of fossils, of course has to recognize that fossils may be imperfectly preserved and are subject to confusing displacements and distortions for which allowance has to be made. They cannot be studied quite like recent forms, where all of the parts are in place.

I have been in touch with Dr. Mortensen for many years by correspondence or by personal contact, and admire his skill and zeal as an investigator. Nevertheless we both feel that cordial relations should not prevent, or be affected, by the free discussion of differences of opinion.

A list of publications cited is given at the end of this paper. In the text they are ordinarily referred to by date of publication, but my *Phylogeny of the Echini and studies of Arbacia* are referred to so often, they are usually recorded as *Phylogeny and Arbacia* paper.

Dr. Mortensen in his great memoir on the *Cidaroida* (1928a, p. 40) expresses doubt whether variations such as Prof. René Koehler has described in his extensive memoir on variation in Echini,<sup>1</sup> and I have described in my *Phylogeny and Arbacia* paper, have any general bearing on morphology and phylogeny. I think that an important aspect of a study of variants is that they often do throw light on morphology, as indicated by cases made use of in this paper.

As stated, Dr. Mortensen considers it doubtful whether variations in Echini have a bearing on phylogeny. I have shown in Echini (1899, 1912, 1914, 1927) that *Arrested variants* have characters which are typical of less specialized species of the genus, or less specialized genera of the family. *Progressive variants* have characters which are typical of more specialized species in the genus. *Regressive* and *Parallel variants*

<sup>1</sup> 1924. Anomalies, irrégularités et déformations du test chez les échinides, Ann. inst. océanogr.; new ser., 1, fasc. 5, p. 159-480, 32 pls.

have characters comparable to those typical of more or less remote allies. Such variants have been found in studies of ocular and genital plates, in the number of elements in a compound ambulacral plate, in the number of columns of ambulacral and interambulacral plates in an area, and in the structure of the perignathic girdle. It is felt that these variants have a direct bearing on phylogeny. *Aberrant variants* have characters which are quite abnormal and cannot be correlated with the typical characters in any associated forms, but which are of interest from other points of view. Variation is at the very foundation of evolution and as such deserves careful consideration. (See classification of variation, *Phylogeny*, p. 18-20; *Arbacia* paper, p. 440-441.)

*Bothriocidaris* from the Ordovician of Esthonia is known from three species, including some seven specimens. Previously this genus has been accepted without question as an echinoid by all who have had occasion to study it. Also on account of its age and simple structure, it has been considered a primitive echinoid.

In the work of Aldrovandus, "De Animalibus Insectis Libri Septum," published in Frankfort, 1618, a copy of which is in the library of the Museum of Comparative Zoölogy, a figure of a fossil echinoid is given on the plate facing page 137. I assumed (*Phylogeny*, p. 244) that this figure represented a *Bothriocidaris*. Dr. Mortensen (p. 94) thinks that I was mistaken. I believe he is quite right and I was wrong, though Aldrovandus' figures of his fossil, published in 1606 and 1618, reproduced by Mortensen (1913, figs. 1-2, p. 238-240), do certainly resemble *Bothriocidaris*, especially the figure published in 1618.

In 1895 and 1896 (p. 233-235) I correlated the structural characters of *Bothriocidaris* with those of young developing stages of later Echini, comparing them especially with the characters found in young *Gonicidaris*, as critically and exquisitely worked out by Lovén (1892). In the *Phylogeny of the Echini* a new species was described, *B. archaica*, figs. 1-2, which was based on a specimen in Berlin; this also was the original described by Jaekel in 1894. In the *Phylogeny* and later papers, with further evidence, is elaborated the structural relations of *Bothriocidaris* as a primitive radicle.<sup>1</sup> The fact that I have studied it long and carefully does not prove that my views are correct, but does indicate that the views expressed are not hasty conclusions, and I

<sup>1</sup> As *Bothriocidaris* is discussed in many places in the *Phylogeny*, the pages may be recorded as follows: p. 12, 34, 45, 52, 53; fig. 2, p. 54; p. 57, 58, 64, 69; fig. 22, p. 70; p. 79; fig. 40, p. 80; p. 87-89; p. 148, fig. 162; p. 171, 173, 201, 208-211, 238-244; pl. 1, figs. 1-9; pl. 8, fig. 1. The pages of my *Arbacia* paper in which *Bothriocidaris* is considered are: p. 451, 460, 468, 472, 474, 480, 517, 541, 558.



would set forth the reasons for still considering *Bothriocidaris* a primitive echinoid in answer to Dr. Mortensen's contrary conclusions.

Dr. Mortensen, in his *British Echinoderms* (1927), p. 255, says: "In the oldest known Echinoid (*Bothriocidaris*) the interambulacra have only a single series of plates, and a vestige of this arrangement is still found in the other Echinoids, in the first interambulacral plate always being single. . . ." Again Dr. Mortensen, in his *Postlarval development of some Cidarids* (1927a, p. 375), says: "It can hardly be doubted that the existence of an unpaired primary interambulacral plate at the peristomial border throughout the whole of the Echinoid-class, . . . is an inheritance from the *Bothriocidaroid* ancestor." This, of course, as seen in the young (my fig. 10), before the primordial interambulacral plate has been resorbed in development, as usually occurs in Regular Echini. Shortly after the publication of that paper he wrote me that he felt that *Bothriocidaris* could not be considered an echinoid. He verbally expressed the same view when we met in London, previous to his trip to Leningrad to study the material of *Bothriocidaris* there preserved.

Dr. Mortensen's paper is divided under three heads: I. Remarks on the structure of *Bothriocidaris*; II. Affinities of *Bothriocidaris*; III. The origin of the Echinoidea. The same order will be followed in the present paper.

#### I. REMARKS ON THE STRUCTURE OF BOTHRIOCIDARIS

Dr. Mortensen says (p. 94) of the ambulacral plates of *Bothriocidaris* that the pores lie not quite vertically, but at an angle of  $45^\circ$  to the vertical. He notes, however, that there is some difference, and in the type specimen of *B. pahleni* Schmidt the pores lie nearly vertical. In Mortensen's fig. 1.1, p. 95, of *B. pahleni* the ambulacral pores are not actually shown, as is stated, but the perforate tubercles for attachment of spines are shown, as is not stated. According to my observations, in *B. archaica* Jackson, the pores are very nearly vertical in position (figs. 1, 2). High, hexagonal ambulacral plates with pores nearly superposed is the character of young *Goniocidaris* (Lovén, 1892; *Phylogeny*, p. 57, 58). The same feature of high, hexagonal ambulacral plates occurs, more or less developed, especially adorally, in many clypeastroids and spatangoids. In spatangoids also the ambulacral pores may be vertically superposed to a greater or less extent (*Agassizia*, Lovén, 1874, Plate 30; *Urechinus et al.*, A. Agassiz, 1904, Plate 73, fig. 1; *Metalia*, *Phylogeny*, p. 57).

Mortensen further notes (p. 94) that the ambulacral pores of *Bothriocidaris* "lie in a rather large, round groove, very unlike the pores of any true Echinoid." The surrounding groove is very like the groove of the larger ambulacral plates of *Pholidocidaris irregularis* Meek and Worthen (Phylogeny, Plate 74, fig. 8; Plate 75, fig. 4). It is also similar

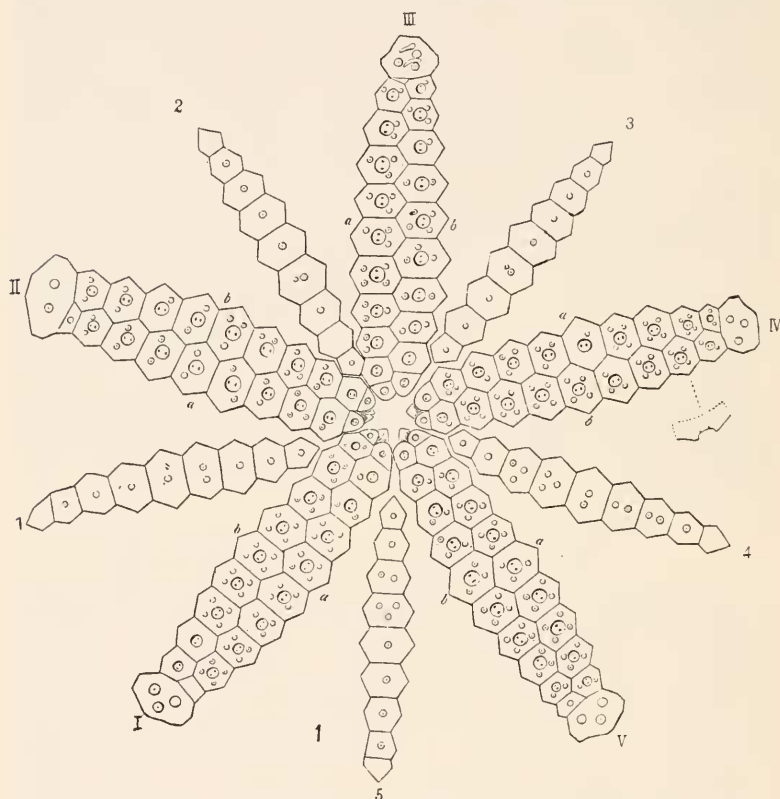


FIG. 1.—*Bothriocidaris archaica* Jackson. Ordovician, Island of Dago, Esthonia.  $\times$  about 2.7. Two rows of peristomal plates; two columns of hexagonal plates in each ambulacrum and one column in each interambulacrum. Orientation based on arrangement of primordial ambulacral plates. (After Jackson, 1912, pl. 1, fig. 1.)

to that of large ambulacral plates of *Pholidocidaris* that I have figured in a paper on the Palaeozoic Echini of Belgium (1929*a*, Plate 5, figs. 6*a*, *b*; Plate 10, fig. 3). The shape of the groove, or peripodium, of *Bothriocidaris* is certainly unusual for Echini, but one may allow for some differences in such an ancient type.

Mortensen's description (p. 95, fig. 2) of tube-feet in *Bothriocidaris* (confirming Lovén, 1883, p. 57) is most interesting. It certainly is very extraordinary that tube-feet, the only ones apparently recorded in a fossil echinoid, should exist in this ancient type. His figure cited is most interesting as showing also spines in place, associated with the perforate tubercles, which, making comparison with his fig. 1.1, are seen to lie in very close association with the peripodium.

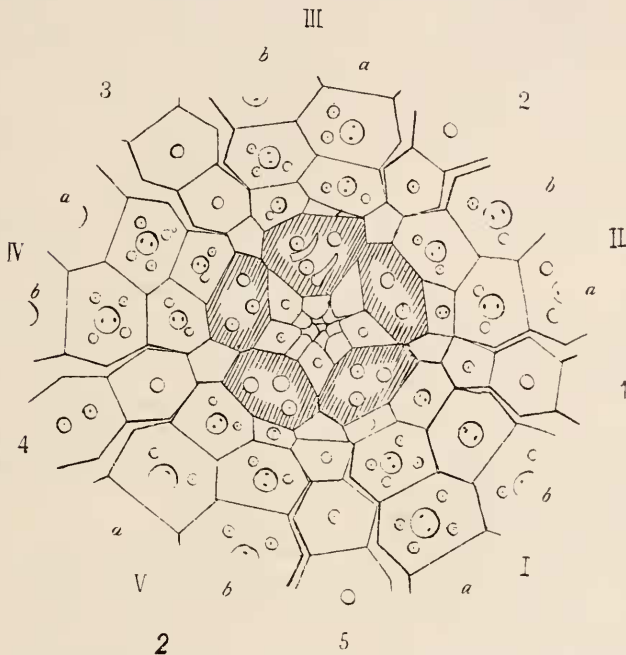


FIG. 2.—*Bothriocidaris archaica*. Same specimen as fig. 1.  $\times$  about 5.1. Apical portion of corona and apical disc. Oculars shaded, meet in continuous ring, genitals dorsal to oculars, small plates in periproct. (After Jackson, 1912, pl. 1, fig. 2.)

As regards the irregularities of some plates in the interambulacra of *Bothriocidaris pahleni* Schmidt and *P. globulus* Eichwald, that Mortensen describes (p. 96, 97, figs. 3.1-3), I have never seen such before, but it does not strike me as anything to be surprised at. The wedge-shaped, or extra plates added, might well be interpreted as a tendency toward two or more columns, which is the character of all other known Echini.

Mortensen (p. 97) speaks of interambulacral plates "divided into two." I know of no evidence for the origination of ambulacral or interambulacral plates in Echini by the division of a preëxistent plate. All coronal plates originate separately on the adoral borders of the oculars as far as known (Phylogeny, p. 28, 64, 362; Arbacia paper, p. 461, 491-492, 528, 541, 557).

The striking similarity of the interambulacrum of *Bothriocidaris* that Mortensen points out (p. 97) to *Proteroblastus* and *Estonocystis* (his figs. 3.4; 10.2-3)<sup>1</sup> may well be looked on as indicating parallelisms, not genetic affinity. The plates of *Bothriocidaris* bear typical echinoid tubercles and spines, which are quite wanting in cystoids.

Mortensen (p. 97, 98, fig. 4) confirms the view that has been held by some others that the madreporite of *Bothriocidaris* is in a radial [ocular] plate. This certainly is a remarkable fact, and it seems that it can only be accounted for as an irregularity of a primitive type. While this feature is different from that of typical modern Echini, it does not thus make an approach to any other known echinoderms. It may be observed that in variants of recent Echini I have described much irregularity as regards the position of madreporic pores in several genera, including three families. Madreporic pores of recent regular Echini are apparently always represented in genital 2, but in aberrant variants they may extend to other genitals, also to oculars and to the interambulacra. This demonstrates that madreporic pores are not necessarily limited to genital 2 where they typically occur and also demonstrates that madreporic pores may exist radially in an ocular plate (Phylogeny, p. 172, 173; Arbacia paper, p. 456).

Mortensen considers (p. 98-101)<sup>2</sup> that the plates lying between the oculars of *Bothriocidaris* cannot be genitals largely because "genital pores are decidedly absent." In such an ancient type it would be quite easy for small genital pores to be filled so as to be unrecognizable, or they may have existed and yet not be visible in external view. I cannot agree with Dr. Mortensen in his statement (p. 100; 1913) that "genital pores are well observable in external view in *Salenia Pattersoni*." I have just had the privilege of examining nine dried specimens of this species in the collections of the Museum of Comparative Zoölogy. In only two of these, which had specially cleaned tests, small genital and ocular pores were seen near the adoral borders of the plates. It seems it can be fairly said that the genital pores of *Salenia pattersoni*

<sup>1</sup> The advantage of the unusual system of numbering text-figures, instead of serial numbers, adopted by Mortensen here and in his *Cidaroida* memoir is not obvious.

<sup>2</sup> P. 99. *The reference Jackson (op. cit., p. 39) should read (op. cit., p. 89).*

A. Ag. are practically invisible externally in ordinary specimens of this rare deep-sea species. I stated earlier (Phylogeny, p. 112, 171, Plate 4, figs. 1, 2) that ocular and genital pores are invisible on the exterior of *Salenia pattersoni*, though plainly seen on the interior. It is not strictly correct that they are invisible externally, but at that time I had only one specimen and then did not succeed in seeing the pores. Mr. Agassiz in the Blake Echini (1883), p. 14, says of *Salenia pattersoni*: "None of the genital pores, with the exception of the madreporic genital, are very distinct." In his Plate 4, figs. 3, 15, 18, 23, the genital pores are shown in each of the five genital plates, but unfortunately, they are somewhat out of place, being too near the centre of the plates.

In the matter of visibility of pores it may be observed that the ocular pores in *Arbacia punctulata* (Lam.), *A. lixula* (Linn.) and *Tetrapygus niger* (Molina) are ordinarily quite impossible to see in exterior view (*Arbacia* paper, p. 454). To suggest, as Mortensen does (p. 101), that genital organs in *Bothriocidaris* may have occurred in connection with the tube-feet seems unwarranted.

In an earlier paper Dr. Mortensen (1912, fig. 1, p. 31) considered the plates adoral to the apical disc in *Bothriocidaris* as genitals. These same plates I considered adapical interambulacral plates (Phylogeny, p. 88). At that time Dr. Mortensen did not mention the absence of pores as any objection to his view of their genital character.

In his discussion of the lack of pores visible in genital plates of *Bothriocidaris*, Dr. Mortensen says (p. 101): "It is in this connection of importance that also the 'ocular' plates are devoid of an ocular pore." It is a rather remarkable fact that in the whole family of the Palae-echinidae, with several genera and many species, that there is not a case known in which ocular pores are visible on the exterior of ocular plates. In *Lorennechinus missouriensis* (Jackson) are described casts of ocular pores seen from the interior (Phylogeny, Plate 41, fig. 2), and I have seen the same in internal moulds of *Melonechinus*, but apparently these pores did not reach the surface, or at least reach it so as to be visible in external view (Phylogeny, p. 89; *Arbacia* paper, p. 454). As ocular pores have not been seen on the exterior of the plates in this large family, where many species and specimens are known, it is not remarkable that ocular pores also are not known in the ancient *Bothriocidaris*.

Mortensen indicates (p. 100) that new interambulacral plates should originate at the adoral border of the genitals. I have shown (and Lambert has shown) over and over again that interambulacral plates in Echini originate on the adoral border of the oculars, and are quite

independent of the genitals (Phylogeny, p. 62; *Arbacia* paper, p. 461, 491-492, 528, 541). Definite demonstration that interambulacral plates originate below the oculars and are quite independent of the genitals is seen in ethmophract spatangoids in which typically genital 5 is absent, and yet the interambulacra are developed below the overlying oculars as usual, fig. 3. Again, in rare aberrant variations, where oculars are misplaced adorally from the apical disc, ambulacra and interambulacra extend adorally from the misplaced oculars just as they typically do from the apical disc (Phylogeny, *Strongylocentrotus*, text-fig. 1, p. 37; *Toxopneustes*, Plate 7, fig. 2). Still additional proof that interambulacral plates develop normally without any contact with

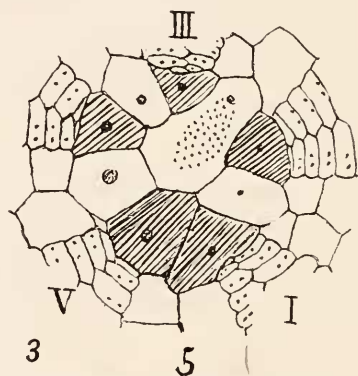


FIG. 3.—*Micrasler coranquineum* (Lam.). Cretaceous, England.  $\times 6.7$ . Oculars I, V meet and cover ambulacra I, V and interambulacrum 5. (After Jackson, 1912, fig. 174, p. 149.)

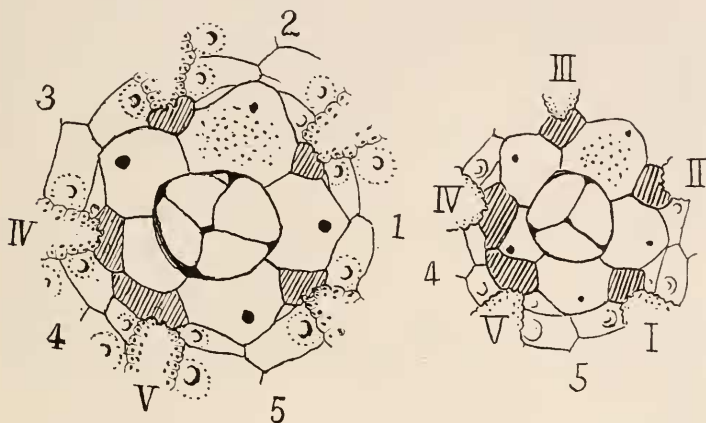
genitals is seen in rare regressive variants in which ocular plates meet on the adoral border of genitals so as to cut them off from contact with the corona as in figs. 4 and 5 (*Arbacia* paper,<sup>1</sup> figs. 24-29, p. 459-461). Or again, in aberrant variants, when a genital is wanting, in partially tetramerous Echini, and as a result, two oculars come in contact, figs. 6 and 7 (*Arbacia* paper, figs. 66-70, p. 539-540). Yet in all these cases interambulacra develop as usual.

Later on in his paper, in considering the origin of the apical system,

<sup>1</sup> The character of oculars meeting below a genital is a feature of *Arbacia punctulata*, fifteen cases of this variation having been found in that species, an average of about one to a thousand. It has also been observed and figured by Koehler in *Arbacia lixula* (Linn.). In other Echini I have found only one similar case in over 50,000 specimens examined.



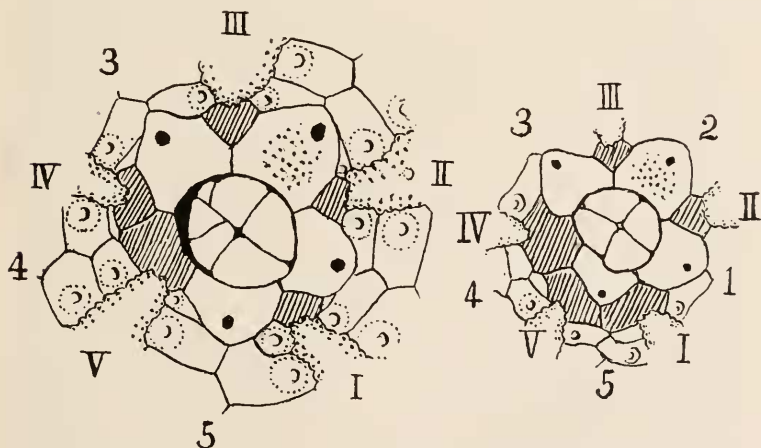
Dr. Mortensen says (p. 119): "that in Echinoids the genital plates always lie adapically to the ocular plates." One might feel that this



FIGS. 4-5. *Arbacia punctulata* (Lam.). Woods Hole, Mass.  $\times 4$ . Variants.

FIG. 4.—Oculars V, IV meet and shut out genital 4 from corona; genital 4 imperforate.

FIG. 5.—Similar to fig. 4, but genital 4 perforate. (After Jackson, 1927, figs. 25, 26.)



FIGS. 6-7. *Arbacia punctulata* (Lam.). Woods Hole, Mass.  $\times$  nearly 4. Variants.

FIG. 6.—Genital 4 wanting, oculars V, IV in contact and cover ambulacrum V, IV and interambulacrum 4.

FIG. 7.—Genital 4 wanting, oculars I, V, IV in contact and cover entirely ambulacra I, V, IV and interambulacra 5 and 4. Genital 5 excluded from corona by adoral contact of oculars I, V. (After Jackson, 1927, figs. 66, 68.)

statement should be considered merely a slip of the pen, but the context would indicate that he intended it. It certainly is not correct, but it is in accord with his theory that oculars and ambulacra rise from below and meet the overlying genitals as a sort of cap-stones to the columns (see p. 506). In the great majority of Palaeozoic Echini, as in *Melonechinus* (Phylogeny, text-fig. 163, p. 149), ocular and genital plates form a continuous ring, adapically all lying in one plane. While in the young of all Recent Regular Echini, as far as known, genital plates lie dorsal to the oculars, in very many species, in development, one or more oculars enter the periproct, or become insert (see p. 499). By this movement adapically such insert oculars come in to the same plane dorsally as the genitals. When all oculars become insert, as in progressive variants, or as a typical specific character, then the oculars and genitals form a continuous ring in one plane on their adapical border, as in most Palaeozoic forms (*Cidaris affinis* Philippi, *Centrechinus*, *Tripneustes*, *Dermatodiadema et al.*, Phylogeny, text-figs. 59, 80, 95, 127).

Ocular plates are essential features in Echini. On the other hand genital plates are of secondary morphological importance as indicated by several factors. A genital plate may be typically absent, as in the posterior area 5 in spatangoids, fig. 3. Or a genital plate may be absent in aberrant variants, as seen in partially tetramerous Echini, my group 17 of nonpentamerous variants, figs. 6, 7 (Phylogeny, p. 45-46, 167; Arbacia paper, p. 538-541, figs. 66-70). Or again, an extra sixth genital plate may be added in aberrant variants, as seen in partially hexamerous Echini, my group 22 (Arbacia paper, p. 548-549, figs. 72, 73). In these several cases the test develops as usual, unaffected excepting by the absence of the wanting genital, or the presence of the super-added genital. Genital pores typically exist in a genital plate, either a single pore to a plate, or in cases, two or more pores may exist in a plate (most Palaeozoic Echini, also parallel variants of modern Echini, Phylogeny, p. 171; Arbacia paper, p. 458, fig. 21). On the other hand, genital pores may typically occur in the interambulacra in certain clypeastroids (Arbacia paper, p. 458). Or apparently in the Cretaceous *Guettaria*, according to Gauthier, genital pores in part may exist in ocular plates as a character (Arbacia paper, p. 458). In Recent Regular Echini I have recorded many cases in which, as parallel variants, genital pores exist in the interambulacra, or in ocular plates (Phylogeny, p. 170, text-fig. 198; Arbacia paper, p. 458, figs. 22, 23). It is evident therefore, that while genital pores usually occur in genital plates, they are not necessarily associated with that structural part. In young



Echini, at an early stage, genital pores have not yet appeared in genital plates (Lovén, 1874, Plate 21; 1892). While in many, perhaps most species, genital pores appear early (in *Strongylocentrotus* at about 5 plus mm. diameter, *Phylogeny*, p. 131, text-figs. 131-134), I have shown that in the primitive genus *Centrechinus* genital pores do not appear until much later, when specimens are about 14 plus mm. in diameter (1914, p. 145, fig. 1). In adult Echini, as arrested variants, one genital, or two, or more, up to four genitals, as observed, may fail to have a genital pore (Arbacia paper, p. 456-457, figs. 9, 19, 20, 24). A genital plate, therefore, develops as usual, whether a pore is present or absent. The madreporic pores may be single, though usually many, and may be limited to genital 2, or may extend beyond that plate as considered, p. 486, 494, 499.

Mortensen suggests (p. 101, fig. 9): "that the whole apical system of *Bothriocidaris* is not really homologous with that of other Echinoids, but rather with the plates at the base of the Cystid calyx." In the cystid figure cited there are four plates in the centre, six in the surrounding row, and seven in the next row. The structure of this Protocrinites as figured by Mortensen differs essentially from that of the apical system of *Bothriocidaris*, fig. 2.

An important feature to consider in relation to the apical disc of *Bothriocidaris* is the point of introduction of new plates of the corona. In all Echini the young last added plates of both the ambulacra and interambulacra are added on the adoral border of the oculars, which is apparently the seat of the placogenous zone (*Phylogeny*, p. 86; Arbacia paper, p. 491-492). In *Bothriocidaris archaica*, the smallest, that is, the youngest ambulacral plates, lie on the adapical border of the area in immediate contact with the oculars (fig. 2). This same feature is shown in Mortensen's figures of *B. globulus* and *B. pahleni* (his fig. 4, p. 98; fig. 6.1, p. 99 and fig. 8.1, p. 100), also my fig. 8. This condition is exactly as it exists in all known Echini. As it is with the origin of ambulacral plates, so also it is with the origin of interambulacral plates. In *Bothriocidaris archaica* (fig. 2) the oculars form a continuous ring, excluding the genitals from contact with the interambulacra. Here the smallest, that is, the youngest interambulacral plates are in contact with the oculars only (fig. 2). This is just as the interambulacra are typically in contact with the oculars only in the posterior area in ethmophract spatangoids (fig. 3) in which oculars I and V meet and cover interambulacrum 5 completely (*Phylogeny*, text-figs. 174-175, p. 149). Also it is directly comparable to rare regressive variants of living Echini in which oculars meet on the adoral border of a genital,

figs. 4 and 5 (Arbacia paper, figs. 25-29, p. 459-460) and the interambulacra abut on the joined oculars. An interesting comparison of rare regressive variants in recent Echini with *Bothriocidaris* is where an interambulacrum in *Arbacia* drops out to a single column of plates adapically and the youngest last added interambulacral plate lies directly against the oculars only as in *Bothriocidaris archaica* (Phylogeny, compare Plate 4, fig. 11; Plate 1, fig. 2).

Instead of oculars meeting in a continuous ring, they may be separated by the genitals, more or less completely as in my fig. 8, after

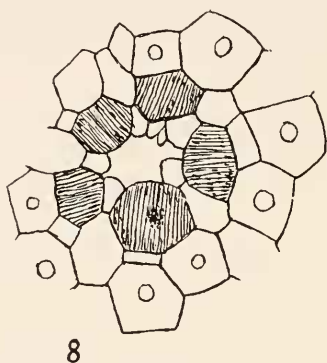


FIG. 8.—*Bothriocidaris pahleni* Schmidt.  
 × 6. Apical disc, oculars shaded, separated by intervening [genital] plates.  
 (After Mortensen, 1928, fig. 8.1.)

Mortensen, of *Bothriocidaris pahleni*. This structure, with ocular and genital plates both reaching the corona, it is to be observed is practically the same as is typical of all other Regular Echini, excepting that the genitals are much smaller than usual (see p. 499) and that in *Bothriocidaris* there is only a single column of interambulacral plates. In this relation the smallest, that is, the youngest interambulacral plates of *Bothriocidaris*, are in contact with the oculars and an intermediate genital. An interesting comparison to this is seen in a rare regressive variant of *Arbacia* in which an interambulacrum has dropped out to a single column of plates adapically, and the last added plate lies against the oculars and intermediate genital (fig. 9). This last contact is practically identical with that shown by Mortensen (my fig. 8) in a camera sketch of *B. pahleni*. It seems that this definite correlation of the point of origin of new plates in the corona of *Bothriocidaris* as

compared with that of all known Echini is strongest evidence of immediate kinship.

The radial position of the supposed teeth of *Bothriocidaris* has been a real stumbling block. Dr. Mortensen's observations help this difficulty by seeming to show that they are not teeth at all. As he notes

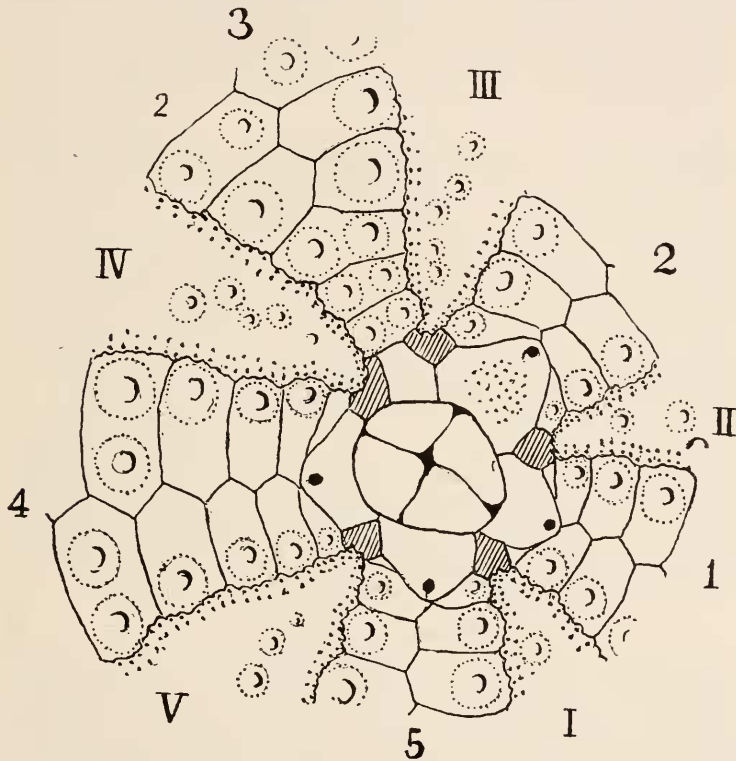


FIG. 9.—*Arbacia punctulata* (Lam.). Woods Hole, Mass.  $\times 4$ . Variant. Interambulacrum 3 reduced to single column for last three plates built, genital 3 of peculiar shape and imperforate. Compare fig. 8. (After Jackson, 1927, fig. 40.)

(p. 102, 109): "There is an indication of tubercles on them, decidedly no striation." Again, in the examination of another specimen from the Reval Museum, Dr. Mortensen says of the "teeth" (p. 121), "It is perfectly evident in this specimen that these plates are of the same nature as the other coronal plates, absolutely not coming from the interior of the test." With all the evidence it seems that these supposed

"teeth" may fairly be considered nonambulacral (that is, bearing no pores) peristomal plates, which are abundant in many Echini (Phylogeny, text-fig. 57, p. 84). They certainly cannot be considered coronal plates as Mortensen implies. I am free to say that one would not expect to find nonambulacral plates adoral to the primordial ambulacral plates in *Bothriocidaris*, but, as they occur in some other Echini, there is no morphological reason why they should not be present.

The giving up of the supposed "teeth" from the evidence that Dr. Mortensen brings forth, does not mean that *Bothriocidaris* was necessarily edentulous, as he assumes (p. 109). It may well have had and probably did have a lantern as in all other Regular Echini, though not at present known. In the Lower Carboniferous genus *Melonechinus*, with 14 known species, the Aristotle's lantern is known in only one species, *M. multiporus* (Norwood and Owen), and there very rarely (Phylogeny, p. 379, Plate 56, figs. 9-10). I recently examined no less than 45 specimens of *Lovenechinus lacazei* (Julien) from the Lower Carboniferous of Belgium, and not a trace of a lantern showed in a single specimen. Yet the lantern exists in several relatively nearly allied forms and doubtless did in the species mentioned.

Dr. Mortensen considers the teeth under the heading peristome (p. 101). To this I would take exception. The peristome is the tissue, plated more or less, or naked, that extends from the basicoronal plates to the mouth opening. The Aristotle's lantern with its associated muscles and the perignathic girdle, as far as existent, are structures quite separate from the peristome (Phylogeny, p. 79, 177).

## II. THE AFFINITIES OF BOTHRIOCIDARIS

In referring to Thiéry's view of *Bothriocidaris* as the young of *Palaeochinus*, as quite untenable, to which I entirely agree, Mortensen (p. 104) indicates that the madreporite and teeth of *Palaeochinus* are interradial. In this he somewhat exceeded the known facts. Recognizable madreporites are rare in the Palaeozoic and have not been recorded in *Palaeochinus*, indeed I have not personally seen one in any of the family of the *Palaeochinidae*. I have thought it possible that some of the several extra pores in genital plates of Palaeozoic types where madreporites are not known, might have served as madreporic pores, as a single madreporic pore occurs in young *Goniocidaris* (Lovén, 1892, Plate 2, fig. 7), also in adult *Habrocidaris* and *Echinocyamus*, and most *Fibulariidae* (Phylogeny, p. 172). As regards the lantern of *Palaeochinus*, while previously unknown in the genus, I very re-

cently described a lantern in *Palaeochinus ellipticus* M'Coy, from the Lower Carboniferous of Belgium (1929a, p. 37, Plate 2, fig. 16). It is incomplete and not in place, but if it were in place the teeth would doubtless be interradian in position. Dr. Mortensen notes (p. 104) that the primordial interambulacral plate has disappeared in *Palaeochinus*. As I have shown, the primordial interambulacral plate has been resorbed not only in *Palaeochinus*, but also in the whole family of the Palaeochinidae (Phylogeny, p. 66; Arbacia paper, p. 472, 474; 1929a, p. 32-33, 36).

Dr. Mortensen says of *Bothriocidaris* (p. 105-106): "That the ambulacra are, in general, of Echinoid character is, of course, undeniable, above all on account of the placing of the radial water-vessel inside the test." The radial water canal is on the inner side of the ambulacral plates of *Bothriocidaris* as well as in all other Echini. On the other hand, the radial water canal is on the outer side of the ambulacral plates in all cystoids and other Pelmatozoa as far as known, and also in all Asterozoa. This internal as compared with an external position of this important structure is a most fundamental character in echinoderm morphology, and is a very strong argument for the echinoid character of *Bothriocidaris*.

Mortensen thinks (p. 107) that the fact that the adoral ambulacral plates on the peristome [the primordial ambulacral plates] of *Bothriocidaris archaica* Jackson are arranged in the sequence Ia, IIa, IIIb, IVa, Vb large, and Ib, IIb, IIIa, IVb, Va small (fig. 1), following Lovén's law, as in the young of Regular (fig. 10) and young and adult of Irregular Echini "is a very weighty argument for the Echinoid nature of *Bothriocidaris*." Allowing this he says (p. 107): "But we do not know whether perhaps the same condition obtains in the protocrinite Cystids, in which case this argument would lose all its weight." This character is not known in any cystoids. If, however, it should be found, it might be evidence for connecting such a type with Echini, but would not, it appears, break its force in regard to *Bothriocidaris*. *Bothriocidaris*, as seen in *B. archaica*, is the only adult Regular Echinoid yet known that does show this character of primordial ambulacral plates.

Dr. Mortensen (p. 107) now seems to feel that the single primordial interambulacral plate at the peristomal border in Echini has little weight, though formerly (1913; 1927, p. 255; 1927a, p. 375) he accepted it as "an inheritance from the *Bothriocidaroid* ancestor." The existence of a primordial interambulacral plate on the peristomal border was first shown by Lovén in clypeastroids and spatangoids in his great work *Études sur les Échinoidées*. Döderlein (1887, p. 17, Plate 9, fig. 6P)



was apparently the first to show the existence of the single primordial interambulacral plate in Regular Echini. His figure of a fragmentary *Goniocidaris canaliculata* A. Ag., 2 mm. in diameter, shows plates of the peristome, the single primordial interambulacral plate, and high ambulacral plates at this early stage. I regret to say that in previous publications I overlooked the discovery of these structures by Döderlein. Lovén (1892) showed the existence of the primordial interambulacral plate with other features in very complete specimens of very young *Goniocidaris* and *Strongylocentrotus*. Lovén's contributions to the knowledge of echinoid morphology and development in these and other structural features include, I think, the most fundamental additions to our knowledge of this subject that have been made. Mortensen in his publication on Postlarval Cidarids, and also in his Cidaroida memoir, as I have earlier recorded (1929), seems to completely ignore, or give but scant recognition to Lovén's highly important work.

The single primordial interambulacral plate is retained in the adult in the basicoronal row in representatives of the Palaeozoic Lepidocentridae and Lepidesthidae (Jackson, 1896, 1912, 1927*a*; Bather, 1918), in the Triassic *Tiarechinus* (Lovén, 1883), in the Recent Echinothuriidae and Arbaciidae (Arbacia paper, p. 468) and in most of the clypeastroids and spatangoids (Lovén, 1874). In most Regular Echini the primordial interambulacral plate, or the same with additional plates, are resorbed in development (Arbacia paper, p. 471-478).

From the primordial interambulacral plate passing adapically, excepting in *Bothriocidaris*,<sup>1</sup> there are typically two plates in the second row, marking the introduction of the second column of plates (fig. 10). This covers the condition in all modern Echini. In Palaeozoic Echini typically there are two plates in the second row, and three plates in the third row, and passing adapically, more columns may be added up to 14, found in *Hyattechinus pentagonus* Jackson, which is the largest number known. These columns, 2-14, are all added perfectly regularly in all types, barring slight individual variations, or mechanical displacements in preservation.<sup>2</sup> The columns, as added, mark successive stages in development of the interambulacral areas as I have shown abundantly in Palaeozoic Echini (1895, 1896, 1912, 1929*a*, fig. 5, Plate

<sup>1</sup> Also excepting the Triassic *Tiarechinus*, which, according to Lovén (1883) has a very peculiar structure, the primordial interambulacral plate in each area being succeeded by three narrow, high plates which fill the rest of the area.

<sup>2</sup> In the order Perischoechinoidea there may be only three columns of plates in an interambulacral area, as in *Lepidesthes wortheni* Jackson and *Meekechinus elegans* Jackson, or species are known characterized by four, five, six, seven, eight, etc. columns in an area, up to fourteen, as noted above.

4, figs. 2, 3). The same developing structure of the interambulacrum is shown by Bather (1918, 1920) in *Pholidocidaris anceps* (Austin). This development of the interambulacrum as indicated by the progressive addition of columns is directly parallel and comparable to the development of the ambulacra, marked also by the addition of columns passing adapically in certain Palaeozoic types as seen especially in the Palaeo-echinidae (Phylogeny, p. 229-232).

Largely ignoring all that has been shown as regards the development of the interambulacrum in Palaeozoic and later types, Mortensen says (p. 107): "if the monoserial condition of the Echinoid interambulacra really were the primitive condition, distinct signs thereof would exist in the young stages of the skeletal development." I agree with him

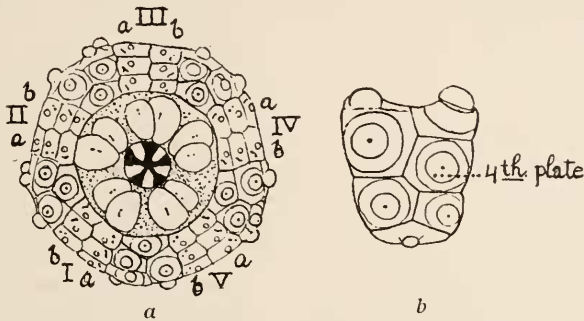


FIG. 10.—Young *Eucidaris metularia* (Lam.), Banda, East Indies. *a*. Primordial interambulacral plates in place, primordial ambulacra plates on peristome. *b*. An interambulacrum of same specimen,  $\times 50$ . Lettering mine. (After Mortensen, 1927*a*, fig. 4, p. 372.)

entirely. They should show and, it appears, they have been shown to exist, first by Lovén and then by many other investigators, including Mortensen himself in his Postlarval Cidarid memoir (1927*a*). Referring to his Postlarval Cidarid paper (1927*a*), Mortensen says (p. 107): It was "a surprise to me . . . to find no trace of the original monoserial condition in the interambulacra of the young Cidarids." As in his paper cited he figured the primordial interambulacral plates in place, succeeded by two plates in the second row in *Eucidaris metularia* (his fig. 4*a*, p. 372, reproduced here as my fig. 10*a*), it is difficult to see how he can make this statement. This the more so because he says (p. 375): "It can hardly be doubted that the existence of an unpaired primary interambulacral plate at the peristomial border throughout the whole of the Echinoid-class, (though resorbed in the course of development in

most of the regular forms), is an inheritance from the Bothriocidaroid ancestor." Mortensen says now: "The only fact which might, perhaps, indicate an original monoserial condition is the slightly larger size of the fourth interambulacral plate" (1928, p. 107-108; Postlarval Cidarids, figs. 4a, b, p. 372, p. 375-376). Again he notes (p. 108): "This fact, however, may equally well be regarded as a reminiscence of an original pluriserial condition." I completely fail to see what this slight difference in size of the fourth interambulacral plate (my fig. 10a, b) has to do with either a former monoserial, or pluriserial condition. It could hardly be evidence, however, for both of two quite different structural conditions as Mortensen implies.

According to Mortensen (p. 108): "The existence of a single primordial interambulacral plate at the peristomial edge in Echinoids is . . . the main argument for seeing in *Bothriocidaris* the ancestor of the Echinoids." While it is truly an essential argument, there are other important features in which *Bothriocidaris* may be considered a primitive echinoid.

Mortensen suggests (p. 108; 1913) that the "existence of only a single primordial plate at the adoral end of the [inter] ambulacra is simply due to lack of space." There is no considerable increase of space in the zone where the second column is introduced (Phylogeny, Plate 2, fig. 1; Plate 3, figs. 9-11; Arbacia paper, figs. 37, 38a, p. 470; Lovén, 1883, Plate 15, fig. 172; Gordon, 1926). Again, the space for the width of the primordial interambulacral plate is, at least frequently, as great, or even greater than the space for the width of the ambulacral area in the same zone. Yet in the ambulacral areas there are always two plates in the basicoronal row, with the exception of the Lower Carboniferous *Melonechinus* in which there are typically four plates in the basicoronal row (Phylogeny, p. 360, Plate 56, figs. 3, 7).<sup>1</sup>

Mortensen also considers (p. 108) that as "the following plates are not paired, but alternating, it would naturally be expected that there should be only one, not two or more plates of [at] the adoral end of the interambulacra." It should be observed in this connection that the coronal ambulacral plates of *Bothriocidaris*, and typically in all other Echini also, are alternating, not paired.

In the Urechinidae and some of the Pourtalesiidae (Lovén, 1883, Plate 21; A. Agassiz, 1904, p. 121-123, 148, text-figs. 159-164, 214; Phylogeny, text-fig. 27, p. 70) the single primordial interambulacral plate is succeeded by a second single plate before the introduction of

<sup>1</sup> In some genera of the Lepidesthidae, in which the structure is incompletely known, in the ambulacral areas there may also have been more than two plates in the basicoronal row.



the second column. Apparently the same character occurs in two species of the Lower Carboniferous *Hyaltechinus* where two superposed single plates at the adoral border of each interambulacral area precede the introduction of the second column of plates (Phylogeny, Plate 24, fig. 4; Plate 25, fig. 1).<sup>1</sup>

Mortensen claims (p. 108): that "the characters of the apical system and the peristome very decidedly speak against regarding *Bothriocidaris* as an Echinoid." With this I distinctly disagree. He says the radial position of the madreporite "is entirely opposed to Echinoid morphology." While the radial position is certainly unlike what one finds in Echini, it does not by that means indicate connections with cystoids, or any other echinoderms that we know. We therefore do not get any help in regard to affinities from the radial position of the madreporite. If the interradial position of the madreporite is to be considered "fundamental in Echinoderms" (p. 108), it is "fundamental" with qualifications, for, as I have shown in aberrant variants in several genera of recent Echini, including three families, madreporic pores may extend beyond genital 2 and exist in other genitals, radially in oculars (see p. 486), and in *Strongylocentrotus* even in the interambulacra (Phylogeny, p. 172-173; *Arbacia* paper, p. 456).

It can be maintained that the apical system of *Bothriocidaris* in most respects is very definitely in accord with that of other Echini. In regard to the large oculars and very small genitals, both reaching the periproctal area, it should be observed that this same character exists as shown by Bury (1896, Plate 7, fig. 34; Phylogeny, p. 87, 90, Plate 3, fig. 5, and schematic fig. 7) in very young *Echinus microtuberculatus* Blainv. Very rapidly in *Echinus*, Bury's fig. 36, the genitals increase actually and proportionately in size and shut out the oculars from contact with the periproct. This feature of all oculars being exsert is the typical character of young Recent Regular Echini. From the condition of oculars all exsert, next in development, the oculars may separate the genitals and enter the periproct, or become insert, one or more to all, in definite sequence (Phylogeny, p. 147-153, *Strongylocentrotus*, figs. 131-139a, p. 129, 132; *Centrechinus*, figs. 88-95, p. 106-107; 1914; 1927, p. 443-453). When oculars are all insert in Recent

<sup>1</sup> In this figure of *Hyaltechinus pentagonus* Jackson the adoral plates are shaded, without intent. In the text this character is not described. The same feature of two single adoral plates superposed is seen better in the new species *Hyaltechinus elegans* Jackson from Belgium that shows developing characters very perfectly. At first I considered the adoral single plate as a non-ambulacral peristomal plate, but it seems that it may more reasonably be considered a small primordial interambulacral plate, succeeded by a second single plate in each area (Jackson, 1929a, p. 27-28, text-fig. 5, pl. 4, figs. 2, 3).

Echini we find, by reversion, or by a second taking on of the character, the condition which is typical of *Bothriocidaris* and most other Palaeozoic Echini (*Lovénechinus*, *Melonechinus*, *Perischocidaris et al.*) that all oculars and genitals meet the periproct in a continuous ring of plates. The relatively very small size of the genitals and large size of the oculars of *Bothriocidaris* is, apparently, a unique feature in an adult echinoid, but this appears to be a primitive condition for, as stated, it is comparable to very young *Echinus*. Usually in Echini the genitals are much larger than the oculars in Palaeozoic as well as in later types. In the Recent deep-sea genus *Dermatodiadema* (A. Agassiz, 1904, Plate 28), however, the broadly insert oculars nearly equal or surpass the genitals in size.

The periproct of *Bothriocidaris* is more or less completely occupied by small plates, which bear tubercles, and are comparable to those seen in many other Echini. They are closely similar to the plates found in the periproct of young cidarids, as figured by Mortensen (1927*a*, fig. 5*b*, p. 373). Mortensen (p. 122) compares the periproctal plates of the Reval Museum specimen of *Bothriocidaris pahleni* with the periproctal plates of cidarids.

Mortensen says of *Bothriocidaris* (p. 108-109): "In the peristomial region the exclusion of the interambulacra from the peristomial border is a fact hard to reconcile with Echinoid morphology." It is not obvious what he means by this statement. As I understand the peristome, it is the tissue plated more or less, or naked, that extends from the base of the corona to the mouth opening and not including the lantern (Phylogeny, p. 79-86). In *Bothriocidaris* the peristome is plated with two rows of ambulacral plates, the primordial ambulacral plates and one additional row.<sup>1</sup> Next comes the base of the corona, with a single plate in each interambulacral area and two plates in each ambulacral area, forming the basicoronal row. This character of the peristome and the base of the corona of *Bothriocidaris* (fig. 1) is closely comparable to that of young *Phormosoma*. As Mr. Agassiz says (1904, p. 79, figs. 131, 132): "One cannot fail to be struck with the *Bothriocidaroid* structure of the actinal system of young *Phormosa* (Plate 43, figs. 3, 5)." Again the peristome of *Bothriocidaris* is almost exactly comparable to that of the young of *Eucidaris metularia* (Lam.) as figured by Mortensen himself (1927*a*, fig. 5*a*, p. 373). The only structural difference from this last is that in the *Eucidaris* the two rows of ambulacral peristomial plates do not fill the area and the primordial interambulacral plates at

<sup>1</sup> To these should apparently be added the five adoral nonambulacral plates, previously considered "teeth," but which, according to Mortensen, should be considered plates.

that stage are largely resorbed. At a little earlier stage, however, Mortensen's figure 4a (my fig. 10a), the primordial interambulacral plates are fully in place. The peristome and base of the corona of *Bothriocidaris* again is like that of young *Goniocidaris* and *Strongylocentrotus* (Lovén, 1892), also *Echinus* (Gordon, 1926), excepting that in these cases there is only one row of ambulacral plates on the peristome, instead of two rows. The interambulacra of *Bothriocidaris* therefore extend to the basicoronal row on the peristomal border, as they do typically in the young and also in the adults of all Regular Echini in which the primordial interambulacral plates have not been lost by resorption and also as they do typically in the adults of most Irregular Echini.

In *Bothriocidaris* the demarcation between the coronal and peristomal plates in the ambulacra is not strongly marked (fig. 1) as it commonly is in recent Echini, but this line of demarcation is also not markedly shown in some other fossil types, as especially seen in the Palaeozoic *Palaeodiscus*, *Hyattechinus*, *Lepidesthes* (Phylogeny, Plate 18, fig. 2; Plate 23, fig. 1; Plate 68, fig. 3). This character is particularly clearly seen in my new *Hyattechinus elegans* from Belgium (1929a, text-fig. 5, Plate 4, figs. 2, 3).

Mortensen again (p. 109) brings up the "teeth" of *Bothriocidaris* and their radial position. I think he shows that they are not to be considered teeth and, as stated (p. 493), may tentatively be regarded as nonambulacral peristomal plates. The radial position of what have been called "teeth" is not in itself an argument for cystoid affinities. Also (as I stated earlier, 1929), as Mortensen maintains that the supposed "teeth" may properly be considered plates, one cannot argue, as he does, that the radial position of a nonexistent part (teeth) is evidence against the echinoid nature of *Bothriocidaris*.

Mortensen says (p. 109): "The necessary conclusion from these various fact[s] is then that *Bothriocidaris* cannot be regarded as the ancestor of the rest of the Echinoids; in fact, it cannot be considered as an Echinoid at all." He emphasizes this statement by widely spaced type. This is certainly putting it pretty strongly.

Mortensen expresses the opinion (p. 109) that *Bothriocidaris* is nearly related to diploporite cystoids (his figs. 10.1-3, p. 110). In these cystoids the interambulacra do certainly resemble those of *Bothriocidaris*, but one may consider this as parallelism because of the weighty differences. These cystoids have brachioles, diplopores, an external water canal, unlike all Echini, and nothing apparently corresponding to the tube-feet, ambulacral pores, peristome, apical disc, or tubercles and spines of *Bothriocidaris* and all other Echini.

Dr. Mortensen treats as if assured, the changes necessary to alter a diploporite cystoid into *Bothriocidaris*. As he says (p. 111): "No doubt, we cannot simply unite *Bothriocidaris* with the Diploporite Cystids; there are too many important differences for that. These latter may well partly have been called forth by the assuming of a free-living existence by *Bothriocidaris* instead of the stalked condition of the Cystids. The free-living existence necessitated means of moving about; for this the fingers of the Cystids would not do, and they were replaced by the large tubefeet known with certainty to have existed in *Bothriocidaris*. In connection herewith the ambulacral furrow of the Cystids disappeared from the surface, the radial canal being placed to the inside of the ambulacral plates, as in Echinoids." This statement Dr. Mortensen makes as if it had taken place, without any qualification as to its being a suggestion, a theoretical conception, or even allowing of any alternative. It seems that this view is quite unwarranted by the facts and based on pure speculation.

### III. THE ORIGIN OF THE ECHINOIDEA

Dr. Mortensen (p. 112) is quite willing to accept parallel evolution for *Bothriocidaris* as compared with Echini. Why may it not be equally possible to consider the similarity of the interambulacral characters of certain cystoids to *Bothriocidaris* as cases of parallelism?

Mortensen (p. 113) accepts the view that the progressive additions of columns of plates in the ambulacra of certain Palaeozoic Echini (Palaeoechinidae), passing from the adoral border adapically, represent specialized development; but will not allow the same for the adjacent interambulacra. Both ambulacra and interambulacra, as regards the additions of new plates, are built alike, the new plates in both areas being added on the adoral borders of the oculars, and by this addition the earlier built plates are thereby progressively pushed adorally. It seems reasonable to argue that as the two areas grow alike, therefore the multiplication of columns, representing stages in development, should be read alike in both, passing from the peristomal border adapically as I have shown in numerous cases (1895; 1896; 1912, p. 62-69, 226-232; 1929a, p. 28, 32).

Mortensen says (p. 113): "For answering the question, where to seek the ancestor of the Echinoids, it is essential to make clear which must be regarded as the more primitive type of interambulacra, that with one or few, regular series of plates, or that with many plates not arranged in definite series." Mortensen argues in favor of irregular,

pluriserial plates as the more primitive (1913), as he considers (p. 113) *Echinocystis* and *Palaeodiscus* are "the oldest of all known Echinoids." This, of course, on his assumption that *Bothriocidaris* is not an Echinoid. Both *Echinocystis* and *Palaeodiscus* which Mortensen considers as having pluriserial, irregular plates occur in the upper part of the Silurian, the Lower Ludlow shales of Leintwardine, England. Mortensen perhaps overlooked the fact that I described *Koninckocidaris silurica* Jackson, from the Niagara Limestone of New York State, which is about Middle Silurian and is distinctly older than the Lower Ludlow (see Kayser, Lake, 1893, *Comparative Geology*, p. 74). *Koninckocidaris silurica* has eight columns of plates in an interambulaerum and they are perfectly definitely arranged in regular columns (*Phylogeny*, p. 285-286; Plate 19, fig. 1; Plate 20, figs. 5, 6).

Mortensen says (p. 113): "It may well be said to be a general principle in morphology that the primitive condition is the existence of many plates, their gradual reduction in number and the corresponding specialization of the remaining parts being the sign of higher development." In support of this view he refers to the foot of the horse, but this seems rather far from the Echini. The horse, however, even in the adult retains structural evidence of former polydaactylism, but Echini neither in young nor adult, show any evidence of a former pluriserial condition. In Foraminifera, ammonoid cephalopods, trilobites and many plants, ontogenesis and phylogenesis are both marked by the progressive addition of structural parts, or structural complexity. Mortensen's view of the reduction of parts as "a general principle" is directly contradicted by the development of the disc in ophiurans, in which the early stages and primitive forms have 11 or 21 plates. To these others are added progressively in development until the complicated disc coverings of the more specialized forms are attained.

Mortensen states (p. 114) of *Palaeodiscus* and *Echinocystis* that the plates "are not arranged in regular columns, as is the condition in the later palaeozoic forms [also in the earlier *Koninckocidaris silurica*], is also what might be expected, as the quite *irregular arrangement must evidently* [italics mine] be more primitive than the arrangement in regular columns." What is the evidence for this? To paraphrase his words of p. 107. If the pluriserial, irregular "condition of the Echinoid interambulacra really were the primitive condition, distinct signs thereof would exist in the young stages of the skeletal development." I agree with this absolutely, but so far no evidence from development has been adduced in proof of an original pluriserial ancestor, rather all evidence from development, in both fossil and recent Echini, is in favor



of a monoserial ancestor. Against the evidence from development, Mortensen assumes (p. 113; 1913) "there can be no doubt that the many interambulacral plates represent the more primitive condition." Again he assumes (p. 114) that the "irregular arrangement must evidently be more primitive than the arrangement in regular columns." With these two assumptions as a basis, he looks for an ancestor of the echinoids.

Hawkins, who is an experienced palaeontologist and a keen student of Echini, recently published (1927), with his student, Miss S. M. Hampton, a critical memoir on *Echinocystis* and *Palaeodiscus*. Of both genera they say (1927, p. 582, 588) that the interambulacra are "built of regular columns," though, as the plates are very thin and imbricating, and distortion has ensued from crushing, considerable overlapping and displacement has taken place. According to Hawkins and Miss Hampton, in *Echinocystis* there are four columns of ambulacral plates adorally with alternate primary and occluded plates adapically (1927, fig. 3, p. 586). *Echinocystis* is certainly specialized, not primitive. The critical opinion of Hawkins and Miss Hampton, based on prolonged study, does not uphold Mortensen's view that *Echinocystis* and *Palaeodiscus* are primitive Echini with pluriserial, irregular plates.

Mortensen gives a highly theoretical discussion (p. 114-117) of how one could derive a primitive echinoid with pluriserial interambulacra from *Stromatocystis* (fig. 12, p. 115) by developing a lantern, changing the position of the anus, madreporite, ambulacra, and developing genital plates, all of which seems very easy to him and far from clear to me.

Mortensen thinks (p. 117): "that the Echinoid ambulacral plates really do correspond to the Asteroid adambulacral plates," though definite proof is wanting. He suggests (p. 117) that: "It is tempting to see the homologues of the true ambulacral plates in the inner prolongations from the ambulacral plates which are found in several Cidarids," and also "in the palaeozoic *Hyattechinus*." The prolongations from the ambulacral plates of cidarids, as described in both *Eucidaris tribuloides* (Lam.) and *Phyllacanthus baculosa* (Lam.) (Phylogeny, p. 61, Plate 3, figs. 12, 13) are direct spinose projections from the interior of the ambulacral plates. There is no evidence of sutures to indicate that they could be considered as separate parts, such as Mortensen's suggestion calls for. In the cidarids described there may be one, or several of these projections to an individual plate and they extend adapically for a considerable distance, even to or above the mid-zone. In the Lower Carboniferous *Hyattechinus beecheri* Jackson and *H. rarispinus*

(Hall), both from Pennsylvania (Phylogeny, Plate 24, figs. 5, 6; Plate 26; Plate 23, figs. 2, 7), I described similar spinose projections extending into the interior of the test from the adoral ambulacral plates. Again I have described similar spinose projections in a new species, *Hyattechinus elegans* Jackson, from Belgium (1929a, p. 29; Plate 4, fig. 4g). Still again I have found similar spinose projections in the ventral plates of an undescribed species of *Hyattechinus* from the Pilton Beds of Devon, in the British Museum, no. E 12,262 (1929a, p. 29). In the case of *Hyattechinus* in the several species there is only a single spine on the interior of each adoral ambulacral plate, situated near the perradial suture. These internal spinose projections are apparently trivial structures, with no obvious function, and it is hard to conceive that they have any considerable morphological bearing.

Dr. Mortensen now seems rather suddenly to have changed his view as regards the morphological relations of the spinose projections on the interior of the ambulacral plates of cidarids. In his superb work on the Cidaroida recently published (1928a, p. 35), considering the apophyses of the perignathic girdle of cidarids, which are direct outgrowths from the basicoronal interambulacral plates, without referring to his previous view he says: "Small apophyses also, as a rule, proceed from the inside of the ambulacral plates, all of them or only those at the peristomial edge (Fig. 22); they would appear to be *homologous with the auricles of other Echinoids* [*italics mine*], though none of the lantern muscles are attached to them." The internal spinose projections in cidarids (to which he refers as apophyses) being direct outgrowths from the ambulacral plates have no sutural connection, whereas auricles do have sutural connection. As shown by Lovén (1892) in his remarkable studies of the lantern and associated parts, auricles are separate parts joined by suture with the interior of the basicoronal ambulacral plates of the Centrechinoida. On the auricles are inserted radially (in the Centrechinoida) the retractor muscles of the lantern, whereas in adult Cidaroida these retractor muscles are inserted interradially on the apophyses (Phylogeny, text-figs. 222, 225-230, p. 193; 1929).<sup>1</sup>

As shown by Lovén, in his unique study of young *Gonicidaris* (1892), at an early stage, apophyses have not yet appeared, and lantern muscles are inserted directly on the basicoronal primordial interambulacral plate. This structure is very important in relation to Palaeo-

<sup>1</sup> Following Lovén, I worked out the structure of the Aristotle's lantern with its muscles and the perignathic girdle in some additional types and introduced the term *apophyses* for the interambulacral processes of the perignathic girdle (Phylogeny, p. 177-198, pl. 2, figs. 7-17, 19-21; pl. 4, figs. 3-5, 8-10; pl. 5, figs. 1-12; pls. 12, 27 *et al.*; 1914, p. 146, 155; 1927, p. 484; 1929a).

zoic types, in which, apparently, no perignathic girdle was developed, and by inference lantern muscles were also inserted directly on the basi-coral interambulacral plates (Phylogeny, text-fig. 221, p. 190-193; 1929; 1929*a*, p. 10).

Regarding Mortensen's view (p. 117) that ambulacra started from the ventral side "to which they were originally confined" and extended "over the aboral side, unto the top," all the evidence we have from the addition and growth of plates of *Bothriocidaris* and all other echinoids is that ambulacral plates originate beneath the ocular and from there are pushed down by the adapical intercalation of later added plates (Phylogeny, p. 52).

Dr. Mortensen (p. 118) assumes the existence of diplopores, and then assumes that they disappear, which to his mind accounts for their absence in *Bothriocidaris*. The movement about of the madreporite and the periproct seems to Dr. Mortensen (p. 118) to be easy to understand. To me, it is not.

In brief, Dr. Mortensen's main points against the echinoid character of *Bothriocidaris* are: (1) that the madreporic pores are in a radial plate; this deserves careful consideration; (2) that what have been considered genitals have no visible pores and therefore in his opinion cannot be accepted as genitals; (3) that what have been considered "teeth" are radial in position (he disposes of this by showing that apparently they are not teeth but plates); (4) finally, he is firmly convinced that the primitive ancestor of the echinoids must have had pluriserial, irregular interambulacral plates; this in direct opposition to what is known from stages in development in both fossil and living forms, and again in opposition to expert opinion in regard to the structure of ancient fossil Echini.

In his appendix (p. 122), in describing a new specimen of *Bothriocidaris pahlani* Schmidt, from the Reval Museum, Mortensen indicates that in only one area does an interambulacrum meet an intervening plate [genital] of the oculars. On the other hand, in his fig. 8.1, p. 100, recorded as the same species, and here reproduced as my fig. 8, all the interambulacra meet such an intervening plate. As he says (p. 122): "The fact that interambulacra of *B. Pahlani* are thus now insert, now exsert, is almost definite proof that the species *Bothriocidaris archaica* Jackson, differing from *B. globulus* only in its interambulacra being all exsert, cannot be maintained but is to be regarded only as a synonym of *B. globulus*."

I originally applied the terms *insert* and *exsert* in descriptions of ocular plates to indicate meeting, or shut out from contact with the



periproct (Phylogeny, p. 90). The term may also be applied to genitals which usually meet, but as aberrant variations, sometimes, though rarely, are shut out from contact with the periproct. I have found 67 cases in which a genital plate (usually genital 3, occasionally 4, very rarely some other genital) was exsert, or shut out from contact with the periproct. Such exsert genitals average about one in 5,000 plates observed (Phylogeny, text-figs. 177-184, p. 165; *Arbacia* paper, figs. 30-33, p. 461-463). Dr. Mortensen's use of the terms *insert* and *exsert* is unfortunate. In his application interambulacra *insert* means that the interambulacra come in contact with genitals, and interambulacra *exsert* means that interambulacra come in contact with oculars only. In neither case do the interambulacra have any relations with the periproct, a condition which the terms were originally intended to describe.

*Bothriocidaris archaica* (figs. 1, 2) agrees with *B. globulus* in having tubercles on both ambulacral and interambulacral plates. In this respect both species differ from *B. pahleni* which has tubercles on the ambulacral plates only. In *B. archaica* the oculars meet adorally in a continuous ring, whereas in *B. globulus* the oculars are all separated by the genitals, which thereby meet the interambulacra. Another difference, one that is brought out by Dr. Mortensen's studies, is the fact that in *B. globulus* (also in *B. pahleni*) in the interambulacra there are some wedge-shaped and also accessory plates (his figs. 3.1-3, p. 96), whereas in *B. archaica* the interambulacra consist of a continuous series of single plates without wedge-shaped, or accessory plates (fig. 1).

When describing the species *B. archaica*, it was felt that the continuous ring of ocular plates which shut out the genitals from contact with the interambulacra (fig. 2) is a remarkable character. It is the only known sea-urchin that does have this character in completeness, and I think it is desirable to maintain it as a species on this basis.

*To sum up the characters and relations of Bothriocidaris as a type, passing from the mouth adapically.*

1. Lantern unknown in *Bothriocidaris*, but probably one existed, as in all other Regular Echini (p. 494).

2. What in *Bothriocidaris* have been considered "teeth" in a radial position is an anomaly, unlike any known Echini, or any other known echinoderm. From Dr. Mortensen's studies they appear to be plates and may tentatively be considered peristomal plates (p. 493).

3. The ten primordial ambulacral plates (in *B. archaica*) arranged in the order Ia, IIa, IIIb, IVa, Vb large, and Ib, IIb, IIIa, IVb, Va small

(fig. 1). The same sequence, as originally worked out by Lovén (1874, 1892), exists in the young of Regular Echini (fig. 10) and in the young and adults of Irregular Echini. Nothing comparable known in any other Echinodermata (p. 495).

4. Two rows of ambulacral plates on the peristome of *Bothriocidaris* (fig. 1),<sup>1</sup> directly comparable to the young of *Eucidaris* (Mortensen, 1927*a*, fig. 5*a*, p. 373) and the young of *Phormosa* (Phylogeny, text-fig. 41, p. 80 (p. 500)).

5. In the basicoronal row of the corona of *Bothriocidaris* (fig. 1) two plates in each ambulacral area, one plate in each interambulacral area as is typical of the young of all Echini (fig. 10), or typical of the young and also the adult of many groups (Lepidocentridae,<sup>2</sup> at least some genera of the Lepidesthidae,<sup>2</sup> the Echinothuridae,<sup>3</sup> Arbaciidae,<sup>3</sup> and most of the Exocycloida<sup>4</sup>) (p. 498, 500).

6. Radial water canal within the ambulacral plates of *Bothriocidaris*, as in all Echini. The radial water canal is on the outer side of the ambulacral plates in the Pelmatozoa, as far as known, and also in the Asterozoa (p. 495).

7. Ambulacra of *Bothriocidaris* with two columns of high, hexagonal plates, pores at a high angle, or more or less nearly superposed (fig. 1). Like the young of *Goniocidaris* (Lovén, 1892, Plate 2, fig. 8). The high character of plates like the young of Regular Echini (Döderlein, 1887; Lovén, 1892; Gordon, 1926; Mortensen, 1927*a*) and, at least adorally, like the young and adult of many Irregular Echini. High, hexagonal ambulacral plates exist throughout the area in some types, as in the fossil and recent spatangoid *Cystechinus* (p. 483).

8. Young ambulacral plates of *Bothriocidaris* lie on the adoral border of the oculars (fig. 2) as in all Echini (p. 491).

9. Interambulacrum with a single column of plates (*B. archaica*, fig. 1), or with some tendency to additional plates (*B. globulus*, *B. pahlani*, Mortensen, 1928, figs. 3.1-3, p. 96). This character is represented by a single plate, as in fig. 10 (exceptionally by two single plates superposed), at the adoral border of the corona in the young, or in the young and adult of all known Echini (Phylogeny, p. 170) (p. 496).

The character of an interambulacrum with a single column of plates, or the same with accessory plates, as a parallelism, is seen in some

<sup>1</sup> Also apparently the five adoral nonambulacral plates which have previously been considered teeth.

<sup>2</sup> As known in representative genera, Jackson, 1896; 1912; 1927, p. 468; 1929*a*, text-fig. 5, p. 25; pl. 4, figs. 2, 3; Bather, 1918.

<sup>3</sup> Jackson, Arbacia paper, p. 468, 475.

<sup>4</sup> Lovén, 1874.

diploporite cystoids (*Estonocystis*, *Proteroblastus*, Mortensen, 1928, figs. 10.2-3, p. 110) (p. 486).

10. Young interambulacral plates of *Bothriocidaris* lie on the adoral border of two oculars and an intermediate genital, when the latter separates the oculars (*B. pahleni*, fig. 8, after Mortensen), as is the typical condition in Regular Echini. The similarity is emphasized when as a very rare regressive variant in recent Echini an interambulacrum drops out to a single column of plates adapically, as seen in fig. 9 (p. 492).

Or young interambulacral plates may lie on the adoral border of two contiguous oculars only, when the latter are confluent, meeting below the genitals (*B. archaica*, fig. 2). This is similar to the condition in rare regressive variants of recent Echini in which in part oculars are also confluent on the adoral border of genitals (figs. 4, 5, 7). It is also comparable to the condition in the posterior area in ethmophract spatangoids, in which, as a typical character, genital 5 is wanting and interambulacrum 5 abuts on oculars only (fig. 3). Again the similarity is strongly marked when in very rare regressive variants an interambulacrum drops out to a single column of plates adapically and the last added plate lies against the two confluent oculars only (Phylogeny, Plate 4, fig. 11) (p. 491).

11. Test of *Bothriocidaris* with tubercles, articulated spines and tube-feet as in all Echini, and as is unknown in *Pelmatozoa* (p. 485).

12. Oculars large, genitals very small (fig. 2), as in the very young of *Echinus microtuberculatus* (Bury, 1896, fig. 34) (p. 499).

13. Oculars of *Bothriocidaris* large, separated by the genitals, as in fig. 8 (also *B. globulus*), as usual in Echini, or oculars adorally meeting more or less completely in a continuous ring and thus excluding the genitals from contact with the interambulacra (*B. archaica*, fig. 2). This last is comparable to the condition in rare regressive variants of modern Echini in which oculars, in part, also meet on the adoral border of the genitals, as in figs. 4, 5, 7 (Arbacia paper, figs. 25-29, p. 459-461) (p. 491-492).

Oculars of *Bothriocidaris* in contact with the adapical limits of ambulacra and interambulacra as in all Echini (p. 492).

14. Genital plates small, separating oculars completely (*B. globulus*), or more or less completely (*B. pahleni*, fig. 8), or genitals dorsal to the oculars when latter are confluent (*B. archaica*, fig. 2). No madreporic or genital pores known in genital plates, which has cast some doubt on the character of these plates (p. 486, 492).

15. Madreporic pores of *Bothriocidaris* apparently in a radial

(ocular) plate (III in *B. archaica*). A radial position is not typical of any other Echini, or any other Echinoderm. In aberrant variants of recent Echini madreporic pores, however, besides being in genital 2, may extend to other genitals and radially to oculars (Phylogeny, p. 172, 173; Arbacia papers, p. 456) (p. 486, 499).

16. Oculars and genitals of *Bothriocidaridaris* form a continuous ring of plates, all adapically in contact with the periproct. This character is as usual in the Palaeozoic Echini and also in those later Regular Echini in which all oculars are insert. When genitals separate the oculars the adoral contact with coronal plates is the same as is typical of all Regular Echini (p. 499).

When oculars of *Bothriocidaridaris* meet on the adoral border of the genitals (fig. 2), the contact with the corona is similar to that seen in rare regressive variants of Recent Echini in which in part oculars also meet on the adoral border of genitals as in figs. 4, 5, 7 (Arbacia paper, figs. 25-29, p. 459-460). It is also comparable to the condition seen in the posterior area in ethmophract spatangoids (fig. 3) in which, due to the absence of genital 5, oculars I and V meet and cover completely interambulacrum 5 as well as ambulacra I and V (p. 491).

17. Periproct of *Bothriocidaridaris* composed of small plates, comparable to those of young *Eucidaris* (Mortensen, 1927*a*, fig. 5*b*, p. 373), and is typically Echinoid (p. 500).

18. All the evidence is that *Bothriocidaridaris* was free throughout life, as are all other Echini. On the other hand, the evidence is that all cystoids, as well as all other Pelmatozoa, were attached in the adult, or, if free in the adult, were at least attached in the young.

Hawkins (1929), after a detailed consideration of Mortensen's paper,, closes with the statement: ". . . I, for one, await some evidence that *Bothriocidaridaris* is unworthy to be called an Echinoid, or at least a fore-runner of the class. Until that evidence is forthcoming (and I cannot find it in Dr. Mortensen's memoir), *Bothriocidaridaris* remains for me a representative of the primitive Echinoid type, from which all of the latter [later] forms I know could have been derived, and toward which many of them show, in the decline of their powers, a tendency to return."

For some thirty-four years I have regarded *Bothriocidaridaris* as a primitive echinoid and structurally representing a near approximation to what one may reasonably consider as an ancestral radicle of the group. I have presented much structural evidence, based on fossil and living, young and adult Echini in favor of this view. *Bothriocidaridaris* is the

central figure on which I based my classification of the Echini (1896, table facing p. 242; Phylogeny, p. 209), and from this echinoid I have drawn many conclusions in regard to the comparative morphology of the group. Maintaining these views, I felt called upon to present the evidence for my conclusions as opposed to that set forth by Dr. Mortensen. This I have done, and trust that the facts and conclusions have been presented with fairness to both sides. In addition it is hoped that differences of opinion and criticisms of Dr. Mortensen's views may be accepted by him and others interested in the spirit of seeking for the truth.

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